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PATTERN DEVELOPMENT IN MAMMALS AND BIRDS

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THE particular coloring of mammals and birds is produced by two factors—pigmentation and the physical structure of the hair or feathers. Both are often present together. In certain mammals, for example the golden mole (*Chrysochloris*) and the European Galemys, a beautifully iridescent sheen is produced by the reflection of light rays having a certain angle of incidence upon the hairs which themselves contain pigment of a characteristic color. In the duckbill (*Ornithorhynchus*) the same thing is found. The peculiarity of feather structure that causes iridescence is largely developed in certain families of birds, as the hummingbirds and the pigeons (see Strong, 1904, for an account of the feather structure).

It is not my purpose to discuss the *use* of this iridescence to the bird, beyond stating my belief that it is in part at least for sexual display, as no one can doubt who watches the male street pigeon strutting before his mate. With amorous coos and lowered head, he confronts her and, swelling out his throat feathers, turns about and about, so that the light is reflected from his neck and throat in a sparkle of rainbow hues. It has also been suggested (Thayer, 1909) that iridescence may be a strong factor in concealment, since from the variety of the colors produced the bird is more difficult to resolve from its many tinted environment amid foliage and flowers.

With many birds the characteristic coloration may not be at all that of its pigment. Thus the blue of the male indigo bird (*Passerina cyanea*) is due solely to the physical structure of its feathers which though pigmented with brown, appear blue by reflected light. If, however, a blue feather be immersed in oil and viewed under a microscope by *transmitted* light, it is seen to be *brown*-pigmented. The physical feather-structure of the adult male is thus in this species a secondary sexual character chiefly developed during the breeding period.

The important point at present is, however, that the color effects just described are none the less due to pigment, quite apart from the fact that the apparent color of the pigmented area may be different from the actual color of the pigment (except that iridescence may sometimes be faintly seen in an unpigmented feather).

The use of pigmentation to its possessor is a matter still under discussion and investigation. In many cases it is doubtless the result of purely physical causes and it is quite without the power of the animal to make use of its coloration for outward effect. Thus the beautiful colors inside the shells of some molluscs are never apparent from an exterior view, and are supposed by some to be in part a waste product, the result of metabolism within the organism.

The present discussion has to do only with the external pigmentation of the hair and feathers, respectively, in mammals and birds.

The simplest cases of coloration are those in which the body or its covering is everywhere of the same hue, or nearly so—as in the elephant, the wild buffalo, or the house mouse in which the hairy covering (or hide in the elephant) is of a nearly uniform tone everywhere. So too, the crow, the apteryx, and the nestlings of many birds whose parents show a more highly differentiated style of markings. Such mammals and birds, so far as the development of pattern is concerned, I would consider unspecialized, yet it does not follow that in this

respect they are also primitive, though in most cases I venture to think this may be true. The uniformity of plumage is probably a derived condition in such a species as the Cuban blackbird (*Holoquiscalus assimilis*) in which the duller colored females have yet a yellow patch at the bend of the wing, a style of marking widespread among allied forms. The adult males, however, have lost this and are wholly black. Gadow as well as Keeler (1893) conclude that among related species in which there is a tendency to differentiation of the coloring the end result of the stages through which the species may pass is the production of a wholly black bird. In general a wholly black condition is no doubt to be considered as a derived rather than a primitive state among birds whereas a uniformly dull plumage of a brownish or grayish tone is probably in most cases primitive. Among mammals the same is probably also true, for in both the black condition indicates either an excessive production of the black over other associated pigments, or a loss of the power to produce the latter, whereas the neutral gray or brownish coloring is due to a more even mixture of such pigments.

As pointed out by Professor W. E. Castle, the "ticked" pattern of the hairs of mammals is probably primitive, and it is certainly very widespread. It is well illustrated, for example, by the house mouse (*Mus musculus*) or the wild guinea-pig (*Cavia*), in which three separate pigments occur as granules in the individual hairs—yellow, chocolate, and black. These three in their normal mixture produce a neutral gray tint—mouse color—and an examination of this type of coat usually shows that some hairs are wholly black, others dark at base barred with black and yellowish near the tip.

There are two ways in which patterns may be developed from a uniformly tinted covering of hair or feathers: (1) by a local change in the relation of the associated pigments so that in certain areas only one or two sorts are produced instead of three, or only one; (2) by a failure to

develop pigment at all in certain places, so that a white or unpigmented area is produced.

It is not rare among mammals to find that one or more of the characteristic sorts of pigments are not produced in certain individuals and probably the factor or factors for these are lost altogether from the somatic and sex cells alike. Such variations may be perpetuated through inbreeding and so no doubt have arisen sundry domestic color varieties of animals and plants. For example, in the course of experiments with color varieties of the house mouse (carried on some years since with Professor W. E. Castle) we found that the chocolate-colored mice which we bred as extracted recessives from black mice, contained only chocolate pigment in their hair, whereas in the black parents both black and chocolate pigments were present, but the black masked a chocolate pigment. Moreover, the chocolate mice always bred true to that color, but if bred back to the black parents, gave black young or both black and chocolate in Mendelian proportions, according to the nature of the matings. The interesting point here is that the chocolate mouse once produced, through the loss of its black-and-gray-pigment-potentiality, can transmit no other pigment character but the chocolate. What causes the occasional production of an individual in which one or more of the characteristic sorts of pigment is absolutely lacking is still unexplained. Nevertheless it is of frequent occurrence not only among domesticated species, in which the natural conditions of life are so greatly modified, but also in species in a state of nature.

A skunk normally marked, but chocolate instead of black, a raccoon likewise of normal pattern but the pigmented areas yellow, are merely examples of the dropping out of the factor for black pigment from the normal combination of the two. Such specimens are of occasional occurrence, and examples are in the museum of the Boston Society of Natural History. Similarly are produced red woodchucks or muskrats, or wholly yellow field

mice (*Microtus*). Melanism commonly results through an excess of black pigment which may mask a second pigment. Thus the black hairs of the black variety of fancy mouse commonly contain a considerable amount of chocolate pigment as well, and so of the hairs of the black-appearing skunk. A black mouse thus does not contain the yellow pigment, while the chocolate pigment is largely masked in general view by the black. In other cases it may be that black pigment alone is present.

It is probable that many cases of dichromatism among animals are explicable as similar cases in which one or other of the pigments normally present becomes to a greater or less degree inactive. Thus red forms of certain blackish or dull-colored bats (*e. g.*, the small *Molossus* of Cuba) are apparently the result of the dropping out of the factor for black pigment or its great reduction. The red and gray phases of the screech owl (*Otus asio*) are probably also explicable as a similar phenomenon.

It is only when this inactivity of one or more of the pigment factors occurs locally on the body that a definite color pattern is produced, in which neighboring areas of the body are of contrasting hues. As an example may be cited the variegated guinea-pigs, whose monotone ancestors are still abundant in a wild state in South America. Professor Castle, through his studies of these patterns in guinea-pigs, first suggested to me in 1903 that there were definite areas of the body which, though contiguous, are independent of each other in their pigment-producing capacity. In this suggestion lies the key to the chief investigation of this paper, namely, the defining of these areas, and a study of their behavior in the development of pattern by the second of the two methods previously given—that is, through the failure of pigment to develop, so that white or colorless areas result. This condition of partial albinism is not uncommon among animals which in their normal condition are completely pigmented. In domestic species it is very general and in them tends to be preserved. It also occurs normally in the shape of defi-

nite white markings in the patterns of many mammals and birds. Magazines of natural history abound with instances of total or of partial albinism among mammals and birds, either of domesticated or of wild species. Some writers have even recognized the fact that such white markings tend to occur in certain parts of the body, as at the tip of the tail or on the forehead. Darwin speaks of the white forehead spot or star, and the white feet so common among horses, and implies that such markings must be of some significance. His statement on hearsay that white-marked horses are more susceptible to poisoning from noxious herbs is, however, uncorroborated. In 1882, W. H. Brewer gathered a number of statistics as to the presence of white marks in horses and cows, but reached no conclusion. He could find no necessary correlation between the presence or absence of white spots in forehead and feet, though it appeared that white marks might be more frequent on one side of the body than the other. But the tentative conclusion that such animals habitually reclined on the side showing the more white, is begging the question.

As briefly stated in my paper of 1904, the important thing is not that white tends to appear at certain places, but the converse, that pigment production is more intense at certain definite centers on the body and the occurrence of white or pigmentless areas is due to the restriction of pigment formation at the periphery of these centers, so that white occurs at their extremities or as breaks between contiguous color patches.

In mammals and birds these centers are typically five on each side of the body, and a median one on the forehead. They appear to be homologous in both groups, though in different species they show varying degrees of modification in their behavior and development. When a reduction of the pigment areas occurs, the appearance is as it were a shrinking of the particular color patch toward its definite center. The reduction may vary to any degree, from that condition in which the break

between two adjacent patches is merely indicated by a white streak to that in which it is reduced to a small spot of pigment, or to zero, when the entire patch drops out, leaving a white area. These patches are wholly independent of each other in the extent to which they may be developed, so that a particular patch may be quite wanting on one side of the body, while its fellow of the opposite side is completely developed. Nevertheless, there is often a marked tendency to bilateral symmetry in such reduction. From a study of partial albinos in which the pigment reduction is considerable, the location of the ultimate centers of these patches becomes possible as well as the determination of their normal extent. I have studied several domesticated species in which white marks are common, with the results briefly detailed below.

When all the centers are fully developed the animal is completely pigmented; when none is developed, it is a total albino. Between these extremes may be found every conceivable degree of development. In an ideal case in which each center is slightly reduced so as to be circumscribed by white, the animal would have a dark coronal or crown patch and a series of five patches on each side separated by a median dorsal and a median ventral stripe. The anteriormost of the lateral patches center at the base of each ear, and each in its greatest development covers the side of the head from muzzle to behind the ear. These I have called the aural or ear patches; the next posterior are the two neck or nuchal patches each of which pigments its proper side of the neck, and extends from behind the ear to the shoulder and anterior edge of the foreleg. When much reduced the patch, as it were, contracts to a small area on each side of the neck, varying slightly in its location among different species. Posterior to these come the scapular or shoulder patches one on each side of the body. Each pigments the shoulder area and foreleg, except (usually) the front edge of the upper part of that member. This patch shows interesting slight variations in the extent over which it spreads in different

species. Centering nearly at the lower part of the back are the pleural or side patches, each of which pigments the area from the shoulder to the lumbar region and anterior part of the hind leg of either side. Last of all, the two sacral or rump patches, each of which on its respective side pigments the buttocks and tail. In most species these two patches are so closely associated that they tend to remain fused dorsomedially, so as to give the appearance, when reduced, of a single median patch at the base of the tail. Their frequent bilaterality, however, indicates the dual origin of such median patches. Each of the lateral patches in its complete development extends from the mid-dorsal to the mid-ventral line or those of opposite sides may overlap slightly. Reduction usually first appears mid-ventrally.

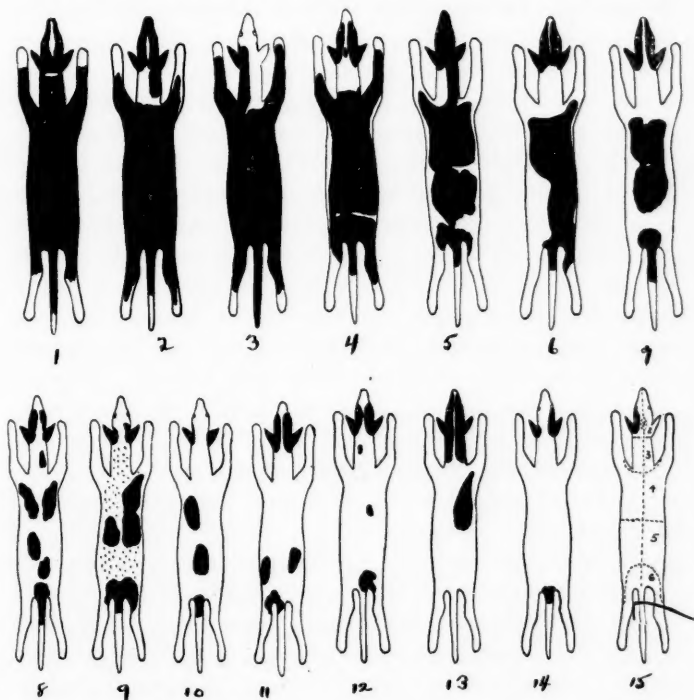
It is probable that the retinas should also be considered as an additional pair of patches, since morphologically the eye is of dermal origin, and there is sometimes seen a tendency to the formation of a small circumorbital patch, which appears to break from the ear patch when this is largely reduced.

Pocock (1907) has pointed out that in black-and-tan dogs the tan appears about the muzzle, along the sides and on the limbs, while the blacker portions are more dorsal. It may be added that in tricolor hounds, in which the several primary patches are reduced, these are often tan color at their several peripheries and black centrally. In both cases, the explanation is simply that pigment formation is less intense the farther away from the primary centers.

The reason of the division of the body surface into these independent areas of pigmentation does not here concern me. It is no doubt the result of physiological causes, and it is rather suggestive that the several patches correspond externally to important nerve centers or groups of nerves. Thus the eye pigment corresponds to the optic nerve, the aural patch to the auditory nerve, so that these two great external sense organs of the head have each their corresponding pigment patch. The neck

patch corresponds with the group of cervical nerves, the shoulder patch with the brachial plexus, the side patch with the nerves of the trunk, and the rump patch with the sacral plexus. It may be further suggested that the median crown patch of the head corresponds to the pineal eye, a suggestion that is strengthened by the fact that it is more or less obsolete in mammals, just as the pineal gland is vestigial, whereas in birds, which are more reptilian in structure, the patch is usually well defined. At all events it is a median unpaired structure, as are the pineal and the interparietal bone.

Turning now to a more detailed consideration of these pigment patches in sundry species of animals, we may first examine a series of diagrams (Figs. 1-15) of the



FIGS. 1-7. DIAGRAMS ILLUSTRATING PIGMENTATION IN THE DOMESTIC DOG.

FIGS. 8-15. DIAGRAMS ILLUSTRATING PIGMENTATION IN THE DOMESTIC DOG.

domestic dog, all of which are carefully drawn from photographs or from living animals, and are selected from a great number to show various conditions in the reduction of the pigment patches. In these and the other diagrams the black portions represent pigmented areas, irrespective of the actual colors.

For convenience I have called the white stripes demarking these chief or primary patches, "primary breaks," since they are the first indications of a decrease in pigmentation such that two adjoining patches no longer meet. Secondary or further breaks result in a general disintegration of these primary pigment patches, and are apparently more irregular in nature, though often they follow certain fairly well defined lines. The first of the primary breaks generally occur as white patches on the chest or belly, about in the median line. These are not shown in the diagrams, but in most cases should be understood as present. In Fig. 1 the pigment areas show a beginning in reduction. The two aural patches have become separated and their failure to spread to the normal limit in the median line has resulted in a white nose stripe. A short transverse white marking indicates a separation of the neck patch at its anterior edge from the ear patch. Elsewhere the various patches are contiguous; but the extremities of the limbs and tail are pigmentless, as if pigment had failed to spread to the tips of these members in its reduction. In Fig. 2 the same primary break between the ear patches is present, and in dogs it is one of the first and most frequent to appear. The same shrinkage of pigment from the extremities is also seen. The neck patch of the left-hand side, however, has completely dropped out, and its fellow of the right-hand side is reduced posteriorly so that it fails to reach the shoulder patch. Thus a white collar is formed. It is also interesting to see that at its anterior end a distinct constriction is present where the neck patch joins the ear patch of the right side. Fig. 3 shows a somewhat similar condition but the neck patch of the right side as well as

the ear patch is missing, while those of the left side are fully developed. In Fig. 4 both neck patches are missing, so that a white collar is formed. In dogs the neck patch is usually the first to drop out altogether, so that a white-collared dog is of very frequent occurrence. In fox hounds this patch is shown unusually well, either wholly or partly separated from neighboring patches. The separation of the ear patches, wholly or partially, so as to produce a white blaze or line in the middle of the forehead is about as frequent. In Figs. 8 and 12 a single neck spot only (as it happens, in one on the right, in the other on the left side) is still present but so slightly developed as to be only a small island of pigment wholly separate from the neighboring patches.

The crown spot is so often present in dogs as a little oval island, always on the top of the head about in line with the anterior bases of the ears (Fig. 4) that I am convinced it is a primary patch. It is common in bull dogs and bull terriers, and in other breeds is often seen but is so commonly not indicated at all, that it seems probable it is becoming lost, and its area is filled by the ear patches, since these are often separated by a very narrow median line only, which, as in Fig. 13, may continue posteriorly to separate the two neck patches medially as well. In other cases (Figs. 1, 6) the failure of the white nose stripe to extend farther posteriorly may be due to the persistence of this patch.

The demarcation of the side from the rump patches is indicated by the imperfect primary break across the lower part of the back in Fig. 4, while in Fig. 5, a similar primary break farther forward indicates the limits of the shoulder and side patches. In each case the break is incomplete transversely, with a narrow isthmus near the median line. In dogs there is a marked tendency for the ultimate centers of the side and rump patches to be close to the median line, so that the corresponding patches of opposite sides are confluent dorsally. This is especially the case with the rump patches, with the result that it is

very rare to see the two rump centers separated, but instead, as in Figs. 10 and 14, they appear, when much reduced, as a small median spot at the root of the tail. That they were originally paired, there is no doubt, as there is frequently (as in Fig. 9) a deep median notch indicating the median primary break between the centers, or (as in Figs. 11, 12) one of the lateral centers drops out, leaving its fellow of the opposite side. The continued union of the side patches with the shoulder patches is seen in Fig. 7, while in Fig. 9, though the union is still present between these patches of the right side, on the left side the shoulder patch has failed to develop, and the side patch is so reduced that it does not meet its fellow of the right. In Fig. 8 both shoulder patches are present more or less bilaterally equal, and, as frequently, are produced into narrow tongues on to the upper arm. The two side patches in Fig. 8 are also reduced, so as to be wholly separated from each other and from the neighboring centers. They are further interesting in being placed nearly median one behind the other instead of nearly opposite. In Fig. 11, on the other hand, they are far sundered, but this, in dogs, is a much less usual condition. In Fig. 10 a single median dorsal patch represents the slightly developed side patches, but whether this single patch corresponds to one or other of the two centers, or whether the two are actually fused in the dorsal line, I can not yet say.

The shoulder centers, when slightly reduced, are large in dogs, and cover a considerable saddle-shaped area, as indicated in Fig. 5, from near the center of the back forward including the fore leg and part of the fore shoulder. When further reduction takes place the pigment is drawn away from the extremities and the saddle separates from the neck patch (Figs. 2, 6) and then from the side patch (Figs. 5, 9), and finally the shoulder patches separate from each other (Fig. 8). One or other of the shoulder patches may drop out entirely (Fig. 10) or be reduced to a very small spot (Fig. 12) at what may be considered

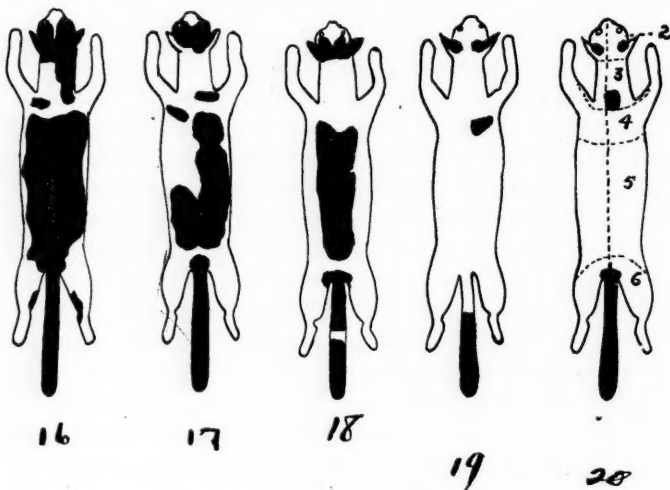
the ultimate center of the pigment patch, near the upper part of the body, near or just back of the shoulder. The ear patches seem to be the last to disappear, and these, too, may be variously reduced or only one may be present (Fig. 15).. The approximate outlines of the patches when fully developed are indicated by dotted lines in Fig. 15, in which 1 is the crown patch, 2 the ear patch, 3 the neck patch, 4 the shoulder patch, 5 the side patch, and 6 the rump patch.

In dogs, there is seldom seen any tendency for these primary patches to divide. What has the appearance of such a tendency is seen, for example, in the coach dog, which is rather evenly flecked with rounded black spots, with often in addition, black ears and more rarely reduced rump patches. Fig. 9 shows such a dog in which both ear patches, one shoulder, both side and both rump patches are sharply indicated, though reduced. In addition there are present on the white body areas between, many small flecks of dark color, evenly distributed, which are clearly not islands separated from the primary patches. Indeed this spotting seems to constitute a wholly different category of pigment formation, in addition to that of the primary patches, which latter I have called "centripetal" pigmentation. As Professor Castle suggests to me, it is probably homologous with the "English" marking or spotted condition of domesticated rabbits, and possibly the dappling of horses is a similar phenomenon. When these spots and the primary color patches are of the same hue, it is not possible to distinguish the two in visual appearance, unless the latter are reduced areally, when, as is sometimes the case in the coach dog, one or more of the primary patches is seen with the spots, as it were, proliferating from its edge. This second element no doubt enters as a factor in the color pattern when the small spots are of a different color from that of the general body surface, as in case of the cheetah (*Cynælurus*) or the leopard and jaguar.

I am inclined to think that the excessive breaking up of

the primary patches, to be considered under the cow, is not a wholly similar phenomenon.

Five diagrams illustrating the domestic cat are shown in Figs. 16 to 20, and are interesting to contrast with



FIGS. 16-20. DIAGRAMS ILLUSTRATING PIGMENTATION IN THE DOMESTIC CAT.

those of the dog, also a carnivorous mammal. The demarcation of the primary patches is usually less sharp than in dogs, but is in general similar. The most common appearance is where the primary breaks occur in the mid-line below, giving a white throat, chest or belly; or the separation of the aural centers produces a white streak on the nose or extends it up between the ears. The ear patches in Figs. 17, 19, 20, show successive reduction, so that at first the hinder margin of the ears, as in dogs, becomes white, then with further decrease in pigment production, the inner bases only are colored. The neck patch has its ultimate center farther back than in dogs so that when much reduced, it is present as a pigmented spot at the very base of the neck or even at the front of the shoulder (Figs. 16, 17). In Fig. 16 the neck patch of the right-hand side is only slightly reduced and is in contact anteriorly with the ear patch, while poste-

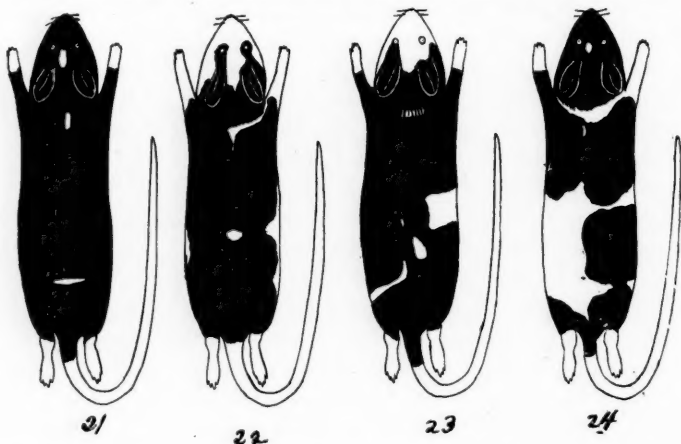
riorly it does not meet the shoulder patch. The left-hand neck patch, however, is quite separate from the neighboring patches and is reduced to a small area at the junction of the neck with the shoulder. It is absent in Fig. 17 from the left side and is represented on the right side by a similar small center, placed far back. In Fig. 20 the neck patch or patches show a reduction to a single small square median patch at the base of the neck, but whether this represents a median fusion of the two lateral centers, or whether one only has persisted and has shifted to the midline, I do not attempt to say, though the former hypothesis seems on the whole more probable.

The shoulder patch in house cats is relatively small, and, as indicated by the indentations in Figs. 17, 18, is of the fore side of the upper arm, but the shoulder patch when fully developed seems to cover the rest of the leg and a small scapular area. It is shown much reduced in Fig. 19, on the right-hand side, and is altogether wanting in Fig. 20. The conjoined shoulder and side patches in Fig. 18 are shown reduced laterally, so as to form a broad median stripe which I take to mean that the ultimate centers are closely approximated dorsally. The neck patch is wholly absent, but both ear patches are present and joined medially. The sacral patches, as commonly, seem fused or at least very close together. There is a small break midway on the tail, which separates off a pigmented tip, a phenomenon which I shall refer to under "centrifugal pigmentation." The side patch is long comparatively, and extends forward to cover the deficiencies of the shoulder patch, as in Fig. 17. Here the left side patch has been reduced at its anterior end, and its separateness from the patch of the right side is indicated by the median indentations. It is often wanting in domesticated cats.

The sacral patches, pigmenting the buttocks and tail, seem to be fused or closely approximated at the root of the tail, as in dogs. I have seen no instance of the crown patch being shown in the cat, though such may occur.

The approximate boundaries of the five bilateral patches are indicated in Fig. 20 by dotted lines; 2 is the ear patch, 3 the neck patch, 4 the shoulder patch, 5 the side patch, and 6 the rump patch.

Among domesticated rodents the pigment patches have been studied in rats, house mice, and guinea-pigs. In all, the same patches appear except that in rats and mice the median crown patch appears to be lost, though in the guinea-pig it is often present. Diagrams of parti-colored mice are shown in Figs. 21-24, and sufficiently indicate



FIGS. 21-24. DIAGRAMS ILLUSTRATING PIGMENTATION IN DOMESTIC VARIETIES OF THE HOUSE MOUSE.

the primary pigment areas. The white spot on the forehead of Fig. 21 indicates a primary break between the two ear patches, and varies widely in different individuals, from a few white hairs only to a large blaze. The inheritance of such a blaze has been studied by Little (1914). The white mark at the base of the neck in Fig. 21 indicates the beginning of separation of the neck from the shoulder patches and perhaps of the two neck patches from each other, because of its longitudinal extension. The white band across the neck in Fig. 23, however, indicates probably only the beginning of a separation of the neck from the shoulder patches, which in Fig. 24 has

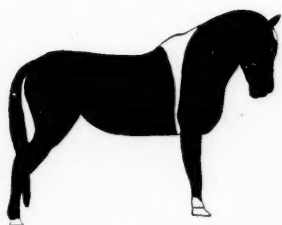
wholly sundered these two areas, so that a white-collared mouse results. The condition shown in Fig. 22 is similar, except that the separation has taken place on the right side only, between the neck and the shoulder patches of but one half of the body. A break between the two neck patches of opposite sides is further indicated in this figure by the deep median reentrant back of the ears.

In all four diagrams the areal restriction of the shoulder patches is shown, but in varying degrees. In Fig. 21, the pigment has not spread to the feet, leaving these white, and so in the other figures, but to a greater degree. A median linear break between the shoulders indicates the restriction of the patches of opposite sides at this point, which in Fig. 22 is more clearly perceptible. The posterior limits of the shoulder patch are further shown in this diagram, by the beginnings of a break between the shoulder and the side patches. In Fig. 24 this break is no longer interrupted, but clearly separates the two areas. Further, the side patch has dropped out on the left. In Fig. 23 an imperfect separation of patches on the posterior part of the body has taken place. On the right-hand side the shoulder patch, which in mice is of considerable extent, has broadly separated from the side patch, while on the left-hand side a long transverse break has taken place between the side and the rump patches, with two island-like white spots between, the anterior of which probably marks the transverse line of stress between shoulder and side patches, the posterior the median line of breaking between the two side patches. A slight indentation in the pigmented area far back on the right side of Fig. 22 points to the beginning of restriction between side patch and rump patch. The separation of these patches by a transverse mid-dorsal break is shown in Fig. 21, and their complete separation on the left side appears in Fig. 23 (the transverse white mark), while in Fig. 24, owing to the failure of the left-hand pleural patch to develop, the two rump patches, both partially separate from each other, are wholly disconnected

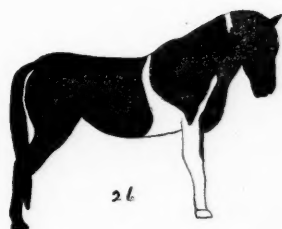
from the former except by a narrow isthmus on the right side. The long tail is usually without pigment, or mainly so where areal restriction is present, and it is seldom that pigment extends far on to the base of this member when the restrictive tendency appears. In the domesticated varieties of rats, the same patches may be distinguished. There is, however, an interesting variety known as the "hooded" rat, in which the ear and neck patches appear to be normal, but a narrow median dorsal area is pigmented for a varying length, sometimes quite to the root of the tail. A separate factor seems here to be involved, producing what may be called a "centrifugal" type of pigmentation, which in many forms of mammals causes a black spine stripe (*Sorex wardi*, *Tupaia tana*, certain forms of *Apodemus*, *Equus caballus*), and others.

Among guinea-pigs the typical primary patches are beautifully shown and may be seen in sundry figures published in papers by Professor Castle on heredity in this animal. The guinea-pig is one of the few mammals yet known in which the median crown patch is visibly present, a character which I take to be primitive.

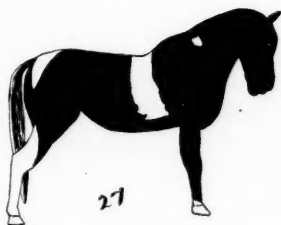
In guinea-pigs the breaking up of the ticked color pattern has progressed under long domestication to an extraordinary degree, so that not only are black, tawny or grizzled animals produced in various shades, but even in the same individual, *the different primary pigment areas may be of different colors*. This fact is of much significance, for it indicates not only the mutual independence of the contiguous color areas, but further points to the manner in which a variegated color pattern may have been acquired. Among mammals the color pattern is in general, not greatly developed in comparison with birds, yet in many cases where some modification has taken place, it is evident that this differentiation is confined to the limits of one or two of the primary pigment patches. Thus in the South American Tayra (*T. barbara*), the head and neck are a grizzled gray, and the breaks occurring in pied individuals show that the grizzled condition



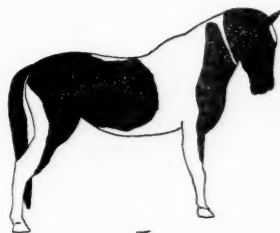
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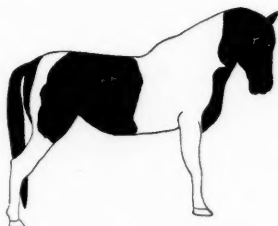
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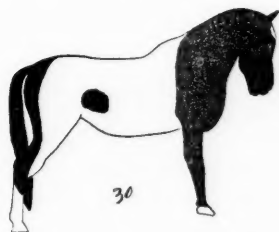
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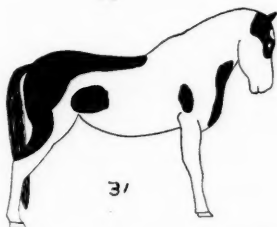
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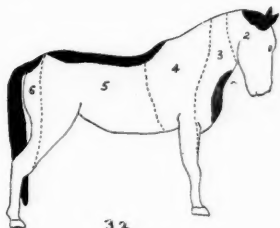
29



30



31



32

FIGS. 25-32. DIAGRAMS ILLUSTRATING PIGMENTATION IN HORSES.

is confined to the aural and nuchal patches only, for elsewhere the animal is black. In this case, too, the black condition is probably derived, for youngish animals are uniformly grizzled, and sometimes, apparently, this is the adult condition as well.

Among domesticated ungulates the same primary patches are to be distinguished in cases where partial albinism renders their bounds apparent, with the exception that in horses, cows and deer I have seen no clear indication of the median crown patch which in mammals is probably obsolescent.

In both horses and cows the patches show interesting and peculiar modifications. A series of diagrams (Figs. 25 to 32) show these patches in "calico" horses, though not so fully as could be wished. The first indications of areal restriction of pigment in horses appear in the shape of a white "star" or round spot in the center of the forehead. This is often accompanied by white at the base of the hoofs, or sometimes the entire foot is white producing the so-called "white stockings." But there is no necessary correlation between these white areas, such as Brewer (1882) tried to show. The white on the forehead may vary from a few white hairs to a broad blaze covering the entire front of the head between the eyes to the muzzle. Sometimes the restriction of pigment is such as to produce in addition to the white star on the forehead, a white spot over each eye, and sometimes these three spots are joined by a narrow unpigmented area. This indicates that pigment production is weak at a spot directly over the eye in comparison with neighboring parts, and this no doubt accounts for the fact that in black-and-tan or other dogs these are the pale spots over the eyes where black pigment is not produced. A white spot over the eye is also characteristic of many rodents.

Next after the restriction of the ear patches and the drawing away of pigment from the feet, the most common

white marking seems to be a primary break, as in Fig. 25, from the shoulder back of the foreleg, which delimits the posterior border of the shoulder patch. In the horse the shoulder patch is large, and differs from that of any mammal I have yet studied, in its great extent forward along the dorsal side of the neck nearly to the head. In Fig. 26 a small break at the back of the neck indicates the beginning of separation between the ear and the neck patches dorsally, and a long tongue of white running upward from the forearm indicates the anterior limit of the shoulder patch. This limit is marked still nearer the dorsal line in Fig. 27 by a white spot on the side of the neck near its base. In Fig. 28 the shoulder patch has entirely dropped out and the white space outlines very nearly its extent. The ultimate center is perhaps shown by the small shoulder spot in Fig. 31.

The area covered by the ear patches extends well on to the upper part of the neck, and in Fig. 29 is shown at its greatest spread, or, as in Fig. 28, cut off by a narrow white collar from the neck patch. The neck patch is remarkable from the fact that in its areal reduction it becomes restricted first dorsally, and the ultimate center of each side is nearly ventral on the throat, so that, as generally seen, the two centers form a single median patch on the front or ventral part of the throat. In Fig. 26 the neck patch is seen to pigment the anterior side of the forearm and is partly separated from the shoulder patch by a long tongue of white. It seems to extend up diagonally to reach the mid-line of the neck for a short distance only, as indicated in Fig. 28, where its bounds are only slightly contracted. In Fig. 29 it is so far lessened as to be absent from the forearm, though still in contact at the throat with the ear patch where, however, a deep indentation locates the dividing line between the two patches. In Fig. 31 a median ventral division of the conjoined neck patches is seen indicated at the upper part of the area, which in this case no longer reaches the ear patches. Still further reduction of both ear patches and neck

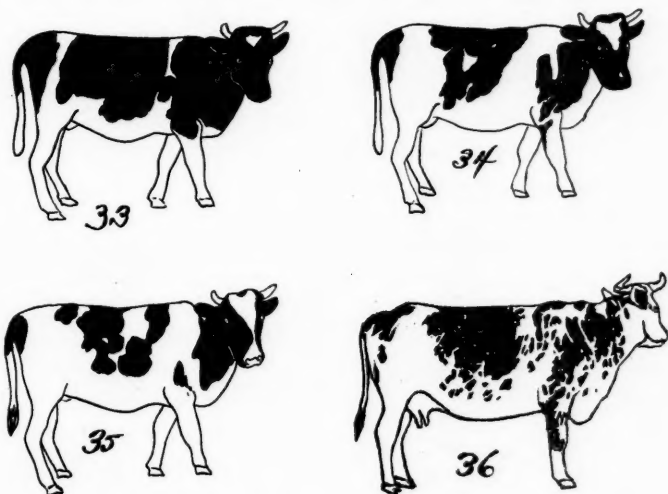
patches is seen in Fig. 32, but, as commonly, the neck patches seem fused in the midventral line. This shifting of the neck centers ventrally is a rather remarkable phenomenon which may have some relation to the manner in which the head is held erect. For this reason it might be expected also in antelopes, and is perhaps evidenced in such a species as the oryx, in which there is a black median line on the throat as though strongest pigment production centered there rather than on the gray sides of the neck. The median reduction of the shoulder patches in horses is sometimes indicated by a white mane.

The rump patches in the horse appear to be much as in other mammals, restricted to the tail and posterior part of the buttocks and the entire foot. In Fig. 30 the patch is shown at nearly its full development, except that it has failed to extend to the entire hind foot. In Fig. 27 it has drawn away still farther but remains in contact with the side patch at one place. In Fig. 29 it is further restricted to the tail and posterior border of the haunches, while in Fig. 32 it covers only the root of the tail and that member.

The side patch is the largest of all and extends from the shoulder to the fore part of the haunches and on to the fore part of the hind leg nearly to the foot, as seen in Figs. 27 and 28, where it is still in contact with the rump patch, or in Fig. 29 where it has become separated. In its further reduction this patch may appear as a small spot back of the ribs or, as often, a curious division takes place, separating the patch into a dorsal area and a lateral one. Occasionally this secondary break appears in a horse which has most of its patches otherwise well developed. In Fig. 31, the pigmented area of the tail, buttocks and lumbar region consists of the conjoined rump patch and a dorsal portion of the side patch, while the *ventral* part of the side patch is present as the oval spot at the groin. In Fig. 30 the latter spot only persists, but in Fig. 32 the dorsal portion of the side patch alone is present as a stripe along the entire back, except where it breaks away posteriorly from the small rump patch.

This peculiarity of the side patch in horses is somewhat paralleled in cows by a tendency to secondary breaking up, though in a different way, as detailed below. It is significant in this connection that in horses and donkeys there is usually a black stripe along the spine from shoulder to tail which may indicate that "centrifugal pigmentation" is also present (see beyond). The dotted lines in Fig. 32 indicate the approximate boundaries of the several primary patches. The crown patch seems to be wanting in horses; 2 is the ear patch, 3 the neck patch, 4, 5 and 6 the shoulder, side, and rump patches, respectively.

Of domestic ruminants I have studied the pigmentation in the cow and show in Figs. 33 to 42 a few of the many

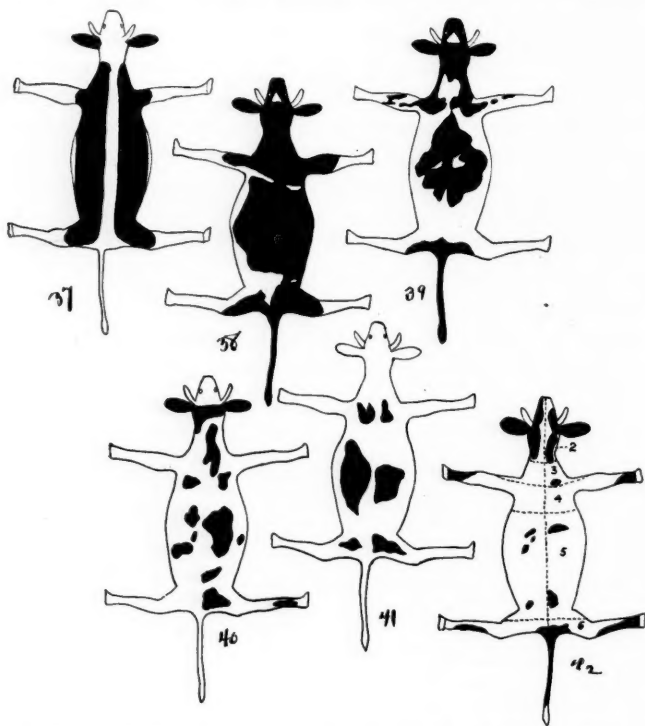


FIGS. 33-36. DIAGRAMS ILLUSTRATING PIGMENTATION IN DOMESTIC COWS, SIDE VIEW.

variations in partial pigmentation. These are all drawn from photographs or from the animals themselves, and are of cows in which, so far as I know, there has been no attempt at breeding for pattern. Two types of spotting may be distinguished in cows: first, that in which the pigmented areas are sharply outlined and solid or at least

practically so; second, that in which there is a greater or less tendency for the primary patches to be much broken up into small islands (as in Fig. 36) by secondary breaks, though the main areas are still distinguishable. I take this second or fragmental type to be a different phenomenon from the diffuse or dappled condition seen in the coach dog or the dappled-gray horse.

In the cow, the ear patches as usual pigment each its proper side of the head to a short distance behind the



FIGS. 37-42. DIAGRAMS ILLUSTRATING PIGMENTATION IN DOMESTIC COWS, AS SEEN SPREAD OUT AND FROM ABOVE.

ears. The point of separation between ear patches and neck patches is indicated by a small break back of the skull in Fig. 38, while the posterior extent is shown by the two ear patches in Fig. 42. These patches usually

draw apart first across the forehead making here a triangular white mark, and on the muzzle, as in Fig. 34. Further restriction broadens these white marks and joins them by a narrow isthmus as in Fig. 35. In Fig. 40, the two patches are still conjoined across the vertex, but are much reduced, that of the right side more than that of the left. In Fig. 42 they have failed to join medially, though fairly well developed longitudinally. Still greater reduction, as in Fig. 37, confines them to the ears, the bases of which appear to be the ultimate centers.

The neck patch in the cow is more extended posteriorly than in the horse, and its center is strictly lateral rather than nearly ventral. It is shown in Fig. 34 somewhat contracted from the mid-line of the throat, but extends squarely back against the foreshoulder at the base of the neck, and is fused near its ventral corner with the small shoulder patch, itself much reduced. As in other mammals it appears to extend in its complete development, to the front edge of the upper foreleg. The animal in Fig. 41 shows a bilaterality in its pigmentation that is rather unusual. What appear to be the reduced neck patches are seen far back at the border of the foreshoulder. In Fig. 40 the left-hand neck patch has dropped out, but that of the right side is still present, though small, and in Fig. 42 it is reduced to a small spot only.

The shoulder patch in cows is remarkably narrow, and compressed between the neck patch and the body patch, whence it extends as usual on to the foreleg. In Fig. 33 a primary break back of the foreshoulder marks the nearly vertical posterior outline of the shoulder patch. In Fig. 34 the separation of this area from the neck patch is all but complete and the patch itself somewhat reduced. Its narrow vertical outline is thus indicated, as well as in Fig. 39, in which there is a narrow tongue-like extension down on to the center of the foreleg.

In its further reduction it appears as a small center at the base of the scapula, as in Fig. 35, or in Fig. 40, in

which both shoulder patches are present, though small. In Figs. 41 and 42 the shoulder areas are wanting. A very common mark in cows is a white belt just back of the foreleg. This is due to the development of a primary break between shoulder patches and side patches, a condition which is nearly realized in Figs. 33 and 38. It is probable that this marking has been more or less fixed through selection in breeding, and this has been the more readily accomplished, since this break occurs in a place which is one of the first in cows to cease pigment production.

The side patch is large and covers the entire lateral region of the body from the scapula to the hips, and on to the front edge of the hind limb. When only slightly reduced, it appears as a blanket-shaped area across the back as in Fig. 38, where it has not wholly broken away from the shoulder and rump patches, or as in Fig. 33, where it has become nearly separated. In its further reduction this dorsal blanket shows a peculiar manner of breaking up into more or less transverse stripes directed slightly backward. The beginnings of these secondary breaks appear in Fig. 39 in which are seen on each side posteriorly two deep indentations at the edge of the patch, whose points if extended would meet the white pigmentless islands already present within the patch. In Fig. 34 a similar series of indentations points to the trisection of the side patch which is realized in Fig. 35. Here is a characteristic which if developed might eventually result in the actual production of white stripes on the body, such as are found, for example, in certain antelopes as the bongo and the kudu. The tendency of the side patch to divide into three, as in these diagrams, is rather marked in cows, and even with further reduction the three centers persist fairly well. The first of these secondary centers is just back of the shoulder patch, the second about over the last ribs, and the third over the lumbar region. In Fig. 40 the first two are present on the left side, with a small spot between, which has become

separated from one or the other of them, while the third or lumbar spot has dropped out. On the right side, the first and second divisions are still fused dorsally, but the lumbar division is distinct. The same three divisions are seen in Fig. 35, better developed, whereas in Fig. 42, the two lumbar are present, one on each side, and considerably in advance of them, what seem to be the remnants of the first division of the side area, the left one of which has further broken up.

The rump patches show no especial peculiarities, but cover the posterior part of the buttocks and hind legs, and the entire feet and tail. Though frequently the two patches of opposite sides are conjoined medially, they are often, under considerable reduction, well separated. The beginning of such a separation appears in Fig. 38, where there is a deep median tongue of white anteriorly, marking the line of union. In Fig. 41 the reduction has progressed still farther so that the two patches are quite sundered medially and do not extend to the tail. In Fig. 40 the patch of the left side has become inactive, and that of the right side is small.

A curious condition not infrequently seen is shown in Fig. 37, in which all the patches are present, but those of the right side are separated from those of the left by a median dorsal white line, showing the distinct bilaterality of these pigment areas. In the figure, the ear patches are so restricted as not to reach the neck patches of their respective sides, the shoulder patches do not extend far on the forelegs, the side patches are reduced ventrally, and the rump patches, though in contact with the side patches, do not pigment the tail or extremities of the legs. A further reduction of pigment areas results in Fig. 41, in which the paired centers of neck, side and rump patches still appear.

The diffuse condition of pigmentation is illustrated in Fig. 36, which is a photograph, inked in. The ear patch is seen much reduced, but pigmenting the ear. The neck patch is of most irregular shape, with several subsidiary

spots separated from its lower border. A clear line separates the neck patch from the shoulder patch, which is also of most irregular boundary. The side patch, at its fore part, is broken into a series of small islands which tend to arrange themselves in lines following the direction of the ribs. The main part of the patch shows a decided tendency to break into the usual three or perhaps four portions. It is common for cows to have patches with very irregular boundaries and tongues of pigment, which may break off into isolated spots in a most bewildering fashion, but even in such cases it is possible to distinguish the main patches of which these form part.

White patches occur in other domesticated ungulates as the pig, the llama, the alpaca, the camel, the yak, the reindeer, and the goat. In the water-buffalo, occasional animals seen in Egypt show a beginning of pigment reduction through the presence of white in the forehead or on the tail. I have had no opportunity to study the markings of these species.

(To be concluded)

INTERNAL RELATIONS OF TERRESTRIAL ASSOCIATIONS

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CONTENTS

- I. Introduction.
- II. Internal activities of the association, as determined by the constitution of the individual organism.
 - A. Ecological constitution of the organism.
 - B. Constitution of the plant in relation to environment.
 - C. Constitution of the animal in relation to environment.
 - D. Internal activities of the association.
- III. Relative influence of different organs with the association—dominance.
 - A. Factors of dominance among animals.
 - B. Criteria of dominance among animals.
 - C. Specialized and unspecialized animals.
- IV. Distribution within the association.
 - A. Distribution in space.
 - B. Distribution in time.
- V. Interdependence of terrestrial plant and animal communities.
 - A. Geographic relations of terrestrial plants and animals.
 - 1. Geographic range: the province.
 - 2. Distribution within the province: distribution of plants and animals into communities.
 - B. Local relations of plant and animal assemblages (relations within the association).
 - 1. Similarity of ecological type of plants and animals.
 - 2. Relative dependence of plant and animal assemblages.
 - 3. Correspondence in distribution within the association.
 - 4. Uniformity of species composition of plant and animal assemblages.
- VI. Summary and conclusions
- VII. References.

I. INTRODUCTION

THE material here presented is based on the writer's studies, during the past five years, of terrestrial associations of plants and animals, mainly in different parts of the prairie region. The particular area chiefly used for illustration in this paper is the sand prairie of the Illinois River valley, plants and animals of which have been studied by Hart and Gleason (1907) and by the writer (1913*b*). A later study has been made of the vegetation of inland sand areas of Illinois (Gleason, 1910); the Lake Michigan beach area in northeastern Illinois has been studied by Gates (1912); beach areas in Illinois and Indiana by the writer (1914*a*). The chief representation of

the sand prairie is the bunch-grass association, well-developed in parts of northwestern, central and north-eastern Illinois, and in northwestern Indiana, in each of which areas, as well as in the sandhills of Nebraska and of eastern Colorado, the writer has studied. Discussions of physical, vegetational and animal aspects of the associations of the central Illinois sand prairie, together with an annotated list of the animal species, with data on food, habitat-relations, life-history, etc., are embodied in the writer's paper (1913*b*), to which constant reference is made. Frequent citations to a more detailed study of local distribution of grasshoppers, in a Michigan area (Vestal, 1913*a*), and to the many associational studies of Shelford, are to be found.

The data which have accumulated relate nearly equally to the botanical and zoological aspects of associational study, but since the subject of plant ecology is at present more advanced than that of animal ecology, it has been possible to treat the vegetational side of the problem very briefly, so that more of the discussion relates to animals and animal assemblages.

The writings most frequently cited are indicated by italic capitals, the full titles appearing in the list of special references at the end of the paper.

The writer wishes to thank Dr. Charles C. Adams, Dr. Max M. Ellis and Dr. H. A. Gleason for suggestions and criticism.

II. INTERNAL ACTIVITIES OF THE ASSOCIATION, AS DETERMINED BY THE CONSTITUTION OF THE INDIVIDUAL ORGANISM

The internal activities of the association may be said to be the sum-total of the activities of all the plants and all the animals which make up the association. Such a sum-total of activities may well be thought of as an intricate and complicated mass of dependencies. It will simplify the treatment of the entire system of relations if the chief dependencies of the individual organism are first discussed. A knowledge of the ecology of the asso-

ciation is built up largely from a knowledge of the ecology of all the organisms which compose it.

A. ECOLOGICAL CONSTITUTION OF THE ORGANISM

The constitution of the organism is the sum-total of those of its characters which enter into relation with environment. These are commonly classified as *structural* and *physiological*. For the purposes of this discussion it would seem preferable to subdivide physiological characters, restricting the term *physiological* to denote those characters concerned with ordinary metabolic processes of the organism, and excluding those having to do with life-history and rates of reproduction (these may be distinguished as *biographical* and *numerical*¹) and also, when dealing with animals, those related to behavior (*psychological* characters). The constitution of the organism in relation to environment will be discussed in terms of these classes of characters.

B. CONSTITUTION OF THE PLANT IN RELATION TO ENVIRONMENT

The environmental influences in the association are of three kinds: (1) physical, (2) plant, (3) animal. Each plant and each animal must obtain from each of these three constituents of its environment certain necessities; it has certain structural and physiological characters which enable it to obtain these necessities, and to withstand adverse environmental influences.

The environmental relations of plants are very different from those of animals. A tabular comparison of these relations has been made by Shelford (*A*: 593). As therein pointed out, structural characters are of greatest importance in the adjustment of the plant to the environment, and plants in a given habitat are likely to have a common structure or growth-form, indicating common or ecologically equivalent physiological conditions within.

Different plants (and different animals), within a com-

¹ Based partly on Forbes', classification of adaptation to food requirements (1909: 292).

mon habitat, are similar in ecological constitution (ecologically equivalent) in so far as their presence is determined by the same environmental conditions. It should be pointed out that there are local environmental differences within the area of the association which allow the presence of differently constituted organisms, and that the entire range of environmental conditions within the habitat is usually much wider than that of the environmental complex selected by a particular organism. The environmental complex of the organism is not the same as the sum-total of environmental conditions within the association. Each organism differs in greater or less degree from others in ecological constitution, and thus selects a different environmental complex.

The physical factors of the environment are of greatest importance in the life of the plant. Plants influence one another directly to only a slight extent. There is usually very little of the social relationship among ecologically similar plants which will compare with such relationships as seen in animals. Competition among plants is mainly a struggle to determine which plants are to be most favored by physical conditions, and it is probably most severe for the physical factor present in minimal quantity. In desert associations plant competition is almost exclusively for water, and extensive root systems are developed. In grassland it is very largely for above-ground space; in forests it is principally for light. The influence of the animal-environment is probably of greater importance than has commonly been realized by plant ecologists; the study of economic entomology and of the effects of grazing upon grasslands is helping to bring about a realization of the importance of animal influence upon plant life.

The structures of plants show frequent and great modification in response to the physical conditions of the environment. These modifications are most frequent and important with respect to the factor present in minimal quantity. Characters which may be associated with

direct plant influence are infrequent. Certain plants which become more abundant as a result of close grazing are equipped with spines, or have acrid or pungent juices; and many other characters may be correlated with animal influence. The structural modifications are most evident in the adjustment of the plant to external conditions, though these are accompanied by physiological characters which are also in harmony with the environment.

C. CONSTITUTION OF THE ANIMAL IN RELATION TO ENVIRONMENT

The animal, like the plant, selects an environmental complex which is of three kinds: (1) physical, (2) plant, (3) animal. Different animals show extreme variation as to the degree in which the different parts of the environment are important to their existence. Endoparasites, for example, are most directly concerned with the animal part of their environmental complex.

The existence of any animal is dependent upon a number of physical factors, all of which must be present in proper degree or quantity. Minimal and maximal quantities of any one of several factors mark the limits of existence of any animal (*A*: 598—law of toleration of physical factors). It is not necessary to consider these factors in detail. The animal reacts to physical environment most evidently by its behavior: psychological characters restrict activities more narrowly than do those of other types. They are accompanied by structural and physiological characters; hibernation, storage of food, etc., are biographical characters correlated with seasonal changes in physical environment. Animals which are subjected to very severe physical conditions may produce a larger number of offspring than those to which physical conditions are favorable. This is an example of correlation of a numerical character with the physical environment.

The plant environment reacts upon and modifies physical and animal environments, and has also direct influ-

ence upon the animal. In addition to its effect in the control of temperature, light and other physical factors, the vegetation constitutes the basic food-supply for the animal community, and also provides shelter and materials for abode (*A*: 601). Cases of direct association between particular plants and particular animals are numerous, but the majority of animals have no direct relation to particular kinds of plants. Behavior characters are in general of greater importance in the relation of the animal to the plant environment, though such relations are not confined to psychological characters.

There are two sets of relations between the animal and its animal environment. These are: (1) *social*, and (2) *antagonistic*. Social relations (*inter-psychology* and *inter-physiology* of Shelford, *A*: 608, *b*) include those between individuals of the same species, and between animals of the same or similar *mores*² (ecologically equivalent animals), in so far as these relations are not antagonistic. Breeding and family relations are the principal activities which come under this head. Behavior characters are of greatest importance, as compared with structural and other characters. The antagonistic relations constitute the *intermores-psychology* and *physiology* of Shelford (*A*: 608, *c*). They are the antagonistic relations between animals not ecologically equivalent, and they are also antagonistic relations within a species and between ecologically similar forms. These relations are probably not greatly concerned with reproduction, but center about the feeding activities of the animal. The existence of the individual animal, in its relation to other organisms, is dependent upon three conditions: (1) it must obtain suitable and sufficient food, (2) it must be free from destructive competition of animals of similar requirements, (3) it must be able to escape or to withstand attacks of other animals (or, sometimes, of parasitic fungi or bacteria). The various characters of the

² *Mores* (Latin for customs, habits) has been used by Shelford (1911a: 30) to supply the need for a term including all physiological and behavior characters of the animal.

animals are correlated with all three of these conditions. The characters are both "adaptive" (fixed by heredity), and regulatory (not fixed).

Following is a synopsis of correlations between the various types of characters and the three conditions of existence, in the relation of the animal to its antagonistic animal environment.

(I) *Characters Which Enable the Animal to Obtain Food*

1. *Structural Characters*.—Animals of selective food-habits often have specialized structures, as in the case of the long tongue of woodpeckers. Animals of non-selective food-habits have mouthparts that are not so highly specialized; thus grasshoppers and cutworms have heavy mandibles for cutting vegetation; tiger-beetles and *Chrysopa* larvæ have sharp piercing mandibles. The whole structure of the predaceous animal, its "action system," is sometimes suggestive of the manner of pursuit or holding of its prey.

2. *Physiological Characters*.—The physiology of animals of different food-habits differs materially. Physiological characters are not apparent, generally speaking, and are secondary to psychological characters. The range of food assimilable by the animal is usually much wider than that selected by it, as is seen when animals of selective habits take new kinds of food when the usual food is exhausted, often thriving seemingly as well as before.

3. *Psychological Characters*.—Selection of food is determined chiefly by behavior characters of the animal. These may be so widely variable that the animal will be virtually omnivorous, as in the case of crickets, or so narrowly restricted that it eats only a single species of plant or animal, as the leaf-beetle *Blepharida*, a sand-prairie insect eating leaves of the three-lobed sumac, and the pentatomid bug, *Perillus*, which feeds on *Blepharida* (cf. *E*: 49, 30). Selection is only one of the many psychological characters relating to food. The behavior characters manifested in obtaining food are of great variety.

With these are accompanying structural and physiological characters, which, however, play a subordinate part.

4. *Biographical Characters*.—These may consist in timing the life-history of the animal with that of the food-species (plant or animal) in such a way that the period of greatest activity of the former coincides with the period of greatest growth or abundance of the latter. This feature may be incidental to seasonal change of physical environment. Whatever its cause, it is very general in an established association, so general that it is seldom recognized. It is of advantage to both animal and food species.

5. *Numerical Characters*.—The rate of reproduction must be so adjusted to its food-supply (plant or animal) "that only the unessential surplus of this food shall be appropriated, leaving the essential maximum product undiminished" (Forbes, 1909: 293). Species of restricted food-habits must remain less numerous in individuals than general feeders, as the available food-supply is very much less.

(II) *Characters Which Remove the Animal from the Competition of Other Forms*

1. *Structural Characters*.—Structures which permit animals to live in varied habitats, to take varied foods, or to time their activities differently, remove each group of animals from competition of all the others, resulting in advantage to all. To that extent the fossorial forelegs of the mole, the long proboscis of the butterfly, and modifications of the eyes of nocturnal animals, are characters which do away with competition. The structural characters are, however, accompaniments of modifications of behavior, and are secondary to the latter.

2. *Physiological Characters*.—Ability to digest food-materials unavailable to other animals is an advantageous physiological character. Thus the leaf-beetle *Chrysomelids auratus*, which lives on dogbane (*Apocynum*), and the "skin-beetle" *Trox*, which eats animal tissues in an advanced stage of decomposition, have few com-

petitors for food. Physiological, as well as structural, characters, are accompaniments to modifications of habit.

3. *Psychological Characters*.—Apparent preference for certain activities, certain habitats, or certain foods, together with peculiar behavior complexes, seem to be of greater importance in removing animals from competition than structural and physiological characters. Highly regulatory habits permit certain animals to adjust themselves to changing conditions of competition.

4. *Biographical Characters*.—Professor Forbes (1909: 295–298) discusses the alternative timing of the active period among close competitors for food. (It so happens that the animals mentioned, having almost identical habits, compete with each other in many ways, besides with respect to food.) In the sand prairie it has been found that different species of certain genera, having otherwise the same habits, differ greatly in life-history. Evidence of this biographical adjustment is more or less complete for two species of *Arphia* (*E*: 21), two or three species of *Hippiscus* (*E*: 21), two species of the milkweed beetle, *Tetraopes* (*E*: 47), and three species of *Proctacanthus*, robber-flies (*E*: 55). In these genera the term of activity of one species is abruptly followed by that of another, the successive periods usually covering most of the summer season.

5. *Numerical Characters*.—When a certain limited food, place of abode, or other desideratum is used by two or more kinds of animals at one time, a numerical adjustment is likely to be found among these competing species. The rate of multiplication of each species must be sufficient to keep up its numbers, to allow it to hold place with competing species. (Too high rates of multiplication, on the other hand, are disadvantageous because of other influences.)

(III) *Protective, Defensive and Concealing Characters*

1. *Structural Characters*.—Animals have various defensive, protective and concealing structures. Stings, beaks, mandibles, teeth, claws, hairs, spines, resemblance

to surroundings in color or form—all are of advantage to animals which possess them. Certain of the interstitial or blowsand animals resemble in color the sand on which they rest (*Cicindela lepida*, *Stachyocnemis*, *Psinidia*, *Spharagemon*; cf. *E*).

2. *Physiological Characters*.—Malodorous and ill-tasting animals are to a considerable degree exempt from attack. This is essentially a physiological modification, though a structural basis in the form of glands may be present. In the sand prairie *Chrysopa* (lace-winged fly), a number of *Hemiptera*, ladybird beetles, soldier bugs (*Chauliognathus*), blister-beetles (*Epicauta*), and others, are ill-tasting (perhaps not to some animals). The skunk's lack of caution is well known.

3. *Psychological Characters*.—Self-preservation in animals depends more upon their activities and behavior than upon special structures. The ordinary methods of resisting or evading attacks of enemies are generally known and need not be discussed. Many specialized instincts have arisen, such as feigning death, or dropping to the ground when disturbed, as seen in many herbicolous beetles.

4. *Biographical Characters*.—It is to the advantage of animal species preyed upon by others if their period of greatest abundance is timed with the period of greatest activity of the animals which feed upon them.

5. *Numerical Characters*.—Animals, as well as plants, must produce a normal excess in numbers which will provide food for other animals and still leave a sufficient number of individuals to continue the species.

It will be noted that the various kinds of characters usually accompany one another, all being parts of a single modification. This modification may have relation to one or to several of the environmental influences (physical, plant or animal) or to more than one kind of antagonistic relation between the animal and others. The modification is not necessarily advantageous to the animal with respect to all or to any features of the

environment, though a large number of characters do result in advantage. Characters advantageous in one relation may be disadvantageous or indifferent in another relation. The origin of the characters is not at present a subject which can be treated in a study of interrelations of organisms (cf. Shelford, 1912*b*: 342). Behavior characters appear to be of greatest importance to the animal in determining its relations with other organisms of the association, though usually these are accompanied by physiological or structural characters. The animal is not *adapted* to a particular status in the association; its ecological constitution determines what place it shall be able to find among the other animals of its surroundings. The relations among the various animals, when a state of equilibrium has been reached, are the result of mutual accommodation on the part of all the animals involved.

D. INTERNAL ACTIVITIES OF THE ASSOCIATION

It has been indicated that the complex of activities within the association is the synthesis of all the activities of the individual organisms. Each plant and each animal is subjected to physical, plant and animal influences. From the extreme complexity of the entire system of relations within the association, it is hardly possible to consider more than one or several of these at one time.³ It is possible, however, to see that each species finds a status within the association, according to its particular combination of internal and external relations. It continues in fairly constant numbers from year to year. A change in these numbers, if at all great, may cause a disturbance in the association, which is quickly regulated by the activities of conflicting organisms (Forbes, 1880). The entire association of plants and animals, by very

³ Very helpful diagrams are given by Shelford (*C*: 167, 168) which illustrate the food relations of land (prairie) animals. There are also diagrams showing food relations of aquatic animals (*C*: 70, 71). Food relations of animals of plains and mountain streams are discussed by Ellis (1914: 122-127; diagram on p. 125). References to studies dealing with interrelations of organisms may be found in the recent handbook of Adams (1913: 123 et seq.).

reason of the conflicting interests, the varying conditions necessary for existence, and the varying methods of response to these conditions, forms a self-contained and self-regulating system of activities.

III. RELATIVE INFLUENCE OF DIFFERENT ORGANISMS WITHIN THE ASSOCIATION—DOMINANCE

The plant ecologist determines which plants in an association are of greatest importance (dominant) by observing which species tend to increase at the expense of others, which are most abundant, most frequent, largest, etc. Competition among plants in a grassland association is mainly for space, and the dominant species are usually determined with considerable accuracy after some study. With the animals the consideration of dominance involves greater complexity. The important relations between conflicting animal species are those in which they obtain food, are removed from competition, or escape enemies. These relations are in each case most directly concerned with food. The plant-eaters of the association thus form a dominant group within the association, since predaceous and parasitic animals, and scavengers in large part, depend upon them for existence. Individual species within the various food-groups, however, present such striking differences in importance, that we can not speak of all plant-eaters as dominant forms, or that all animals of other food-habits are unimportant. It is merely probable that the phytophagous group will contain a larger proportion of dominant species. This appears to be the condition in the bunch-grass association.

A. FACTORS OF DOMINANCE AMONG ANIMALS

The success of an animal species within an association is due to the resultant effect of a large number of factors. Among these may be mentioned number of individuals, size, activity, voracity, concentration of food, rapidity of growth, rapidity of reproduction, and wideness of distribution in space and in time. Dominance signifies more

than mere ability of a species to thrive in its surroundings: the species of greatest influence are those on which the greatest number of other animals depend; thus dominant species are successful, but successful species are not always dominant. Species which are relatively free from competition or which have comparatively few enemies may be successful, but are not dominant, and are usually not numerous. Species which are successful and at the same time extremely abundant, usually form the food of a large number of other animals, as it appears to be the rule that no considerable source of food within the association is left unused. Dominance in a species, then, would seem to include the dependence of other animals upon it, plus the ability to thrive in spite of the drain upon its numbers.

B. CRITERIA OF DOMINANCE AMONG ANIMALS

The factors mentioned as contributing to the success of a species, and the numbers of animals dependent upon the species, are all indications of the degree of its dominance. It appears that another criterion is available, which perhaps expresses the summation of many factors which contribute toward dominance. This is the degree of specialization exhibited by the species in its adjustment to a particular place in the association. Dominant animals appear to be those of moderately specialized habits rather than those of highly specialized, or relatively unspecialized, habits.

C. SPECIALIZED AND UNSPECIALIZED ANIMALS

Each species may be referred to a position in the scale of specialization in habit. The degree of specialization of the species is well seen in the food-habits, though all the habits are to be considered. The most abundant food in the sand prairie is plant material, bunch-grasses. The majority of the plant-feeders are adapted to eat herbage of nearly any kind: they are not restricted to particular species or particular parts of plants. They are non-selective feeders. Grasshoppers, cutworms and certain

leaf-beetles are thus moderately specialized plant-eaters. There are also non-selective predaceous animals, as tiger-beetles and lycosid spiders, which eat any kind of small animal. These are also moderately specialized. The moderately specialized animals carry on the gross metabolism of the association; they constitute the dominant group, and include the dominant species.

Selective feeders belong with the highly specialized animals. In the bunch-grass association *Languria bicolor*, an erotylid beetle, bores in the stems of the composite *Cacalia* (Indian plantain), while *Lygæus bicrucis* (hemipterous) feeds on the same plant; *Perillus circumcinctus* eats *Blepharida rhois*. Others of the association eat selectively. The majority of parasites are greatly restricted in their selection of hosts. Such animals are particularly dependent upon special kinds of food, which in many cases are not available to general feeders. Highly specialized forms are thus enabled to avail themselves of opportunities denied to animals of generalized type; but while they avoid competition by the adoption of special kinds of food, or by special habit of some other kind, they lack the versatility of the less specialized animals, being unable to adjust themselves to changed conditions. They may, therefore, become abundant at times; but as they depend wholly upon one variable condition (perhaps the presence of a particular plant species, which may be quite infrequent) they never can become dominant species. Absolute numbers of the insects which live upon *Cacalia*, for example, are insignificant in comparison with such animals as the grasshoppers.

On the other hand, animals of relatively non-specialized habits would also be ineffective in the association, for whatever field of activity they were to enter, they usually would find already occupied by some animal better constituted for that activity. Such non-specialized forms would assume particular importance only when some animal on which they might feed should become unusually

abundant. Few animals are really non-specialized in habits; many moderately specialized species, however, may on occasion turn from their ordinary activities, perhaps to appropriate a particularly abundant kind of food. Many ants are thus habituated to certain ordinary kinds of food, but are able to eat organic food of almost any sort, and do vary their food with circumstance. When, as frequently happens, some animal species becomes very abundant,⁴ the attacks of a great many species of flexible habits becomes concentrated upon it, and the numbers of the food-species are soon reduced to normal. Animals with non-specialized habits, by taking whatever food is easiest of access, act as regulators of disturbances within the association. A clear exposition of the manner in which species of generalized habits restore unbalanced conditions to equilibrium is given in a paper by Forbes (1883), in which the regulative action of birds upon insect oscillations is discussed.

The animal's status within the association is determined not only by its food-habits, but by the sum-total of its physiological and behavior characters (its mores). The degree of dominance is indicated not merely by the degree of specialization of food-habits, but in all habits, by the degree of flexibility of behavior. An extreme specialization in nearly any behavior character, as habit of abode in the pit-digging ant-lion larva, prevents the species from becoming dominant. The degree of specialization of behavior is thus a convenient criterion of the relative influence of animals in the association. The dominant animals are moderately specialized, and carry on the ordinary work of the association. The highly specialized animals make use of space otherwise unoccupied and food material not demanded by other species. Certain of the first group, with habits more highly regulatory than is usual, with perhaps some few unspecialized forms

⁴ With some animals sudden abundance is a matter of seasonal periodicity, as in the case of May-flies (*Hexagenia*) along the Illinois River (*E*:17). The adults on emerging become a sudden source of food for animals of adjoining terrestrial associations, as the bunch-grass.

in addition, tend, by following the path of least resistance, to act in opposition to forces tending to destroy the biotic equilibrium.

IV. DISTRIBUTION WITHIN THE ASSOCIATION

The association may be subdivided into minor groups of organisms, both in space and in time. Each group, being thus removed from the immediate influence of the others, is to some extent self-contained, having its own environmental conditions, its own assemblage of organisms, and its own system of interrelations.

A. DISTRIBUTION IN SPACE⁵

Different parts of the space occupied by an association present different environmental conditions. In the vertical distribution, four strata, the air (cf. *E*: 73), the plant layer, the surface layer and the underground layer, are usually present. In forest associations, the plant layer is complex, plants of various heights giving rise to minor strata (cf. *A*). In grassland associations the plant layer is relatively uniform. Animals are most numerous, during the feeding activity, in the plant layer. Others find food at the surface or underground. Many of the animals in the air or on the ground move about rapidly from plant to plant. Predaceous animals (while active) are frequently permanent members of air and ground layers, depending for food upon the transient animals and upon members of their own group. The ground stratum is composed of the surface and subsurface layers (*E*: 72), which are not, however, continuous horizontally, but alternate to greater or less extent.

Local variability in horizontal distribution is due partly to local discontinuity of the various strata. This interruptedness is particularly conspicuous in open associations, where the plants do not form a dense growth, but are separated by open spaces. The subsurface area is provided by cover of various kinds, which lies more or less scattered about on the surface.

⁵ Cf. Shelford, *A*, *B*, 1912*b*, *C*; also *D*: 167; also p. — of this paper.

The motility of the animal allows change in stratum, and to some extent and in some animals, in habitat, with change in activity. The food-stratum and the food-habitat are apparently of greatest importance in the relation of the animal to other organisms.

B. DISTRIBUTION IN TIME

Physiological activities of the plants are subject to diurnal variation, and are also greatly affected by variations in weather conditions. The greater part of the animals of an association are active during the day. Others are nocturnal. During the inactive period of the day the animal rests in some more or less sheltered place, perhaps in a burrow or nest. The inactive state is also induced by unfavorable weather conditions.

Seasonal changes in the association are very great in temperate climates, particularly in treeless regions, where the winters are severe. Seasonal changes in the vegetation are marked, certain groups of the plants appearing in successive periods during a summer season, giving four or five successive *aspects* to the plant cover. A corresponding seasonal distribution is observed among the animals of the association (cf. *D*: 175).

Annual changes in the associations are indicated by the very marked differences in the numbers of individuals, in certain species of plants and animals, in successive years. This may be due (1) to fluctuation in the numerical adjustment between different organisms, and (2) to the effect of annually varying phenological conditions upon the various organisms.

Oscillatory irregularities in the association take place at indefinite intervals. The causes and nature of oscillations have been thoroughly treated in several of Forbes's writings (1880, 1883, 1887).

V. INTERDEPENDENCE OF TERRESTRIAL PLANT AND ANIMAL COMMUNITIES

The thesis of the following section is that, in terrestrial climatic or extensive environments, the relations between

the assemblage of plants and the assemblage of animals are intimate and regular of occurrence; so much so that (1) the two are coextensive, (2) the two constitute together a community which may be called a biotic association, (3) neither plant nor animal assemblage usually occurs independently of the other, (4) the geographic distribution of many of the plant and animal species which make up the assemblages are in general correspondence, (5) the species composition of the association, over its range, varies no more widely, relatively speaking, than would an assemblage of plants alone. Perhaps the single view-point of the botanist, on one hand, and the zoologist, on the other, has tended to a neglect of the dual character of the one problem. Probably most botanists and zoologists agree that relations of animals and plants within a habitat are most intimate, and there is a tacit assumption that all the organisms in one place constitute the true system of interrelations, but botanists have spoken of plant communities, and zoologists of animal communities. There are numerous disharmonies and variations in agreement of plant and animal assemblages, but these must not be allowed to obscure general facts of correspondence.

It is recognized that plants and animals of an area of essentially homogeneous physical conditions are interdependent, the animals as a group being wholly dependent upon the plants for food, and many of the plants being directly dependent upon animals, as in the matter of pollination. All are directly or indirectly affected by animals in some way. It is also recognized that the plants are a good index to conditions for animal life, the plant assemblage affecting animals locally in modification of the physical environment, and more directly in providing food, shelter, etc. (*A*: 601). It is further accepted that plants and animals respond to general environmental conditions in similar manner (Craig, 1908). Thus considered, the character of the plant population of an area is an index to general character, or ecological

type, of the animal assemblage. These relations, however, are quite general, lacking detail. Detailed considerations may be *geographic*, including geographic range of species and of communities, and the distribution of species and of individuals into communities; and they may also be *local*, dealing with interrelations of plants and animals within the area of the community.

A. GEOGRAPHIC RELATIONS OF TERRESTRIAL PLANTS
AND ANIMALS

1. *Geographic Range: The Province*.—If one were to plot the geographic range of the plant species found together in a given climatic habitat, a general correspondence in distribution would be made apparent, a large number of the species ranging more or less continuously over a common, rather definite area (cf. Transeau, 1905). The similar ecological constitution of these plants and their consequent selective distribution into similar environmental complexes gives a uniformity to the vegetation over the geographic region in which these environmental conditions are found, and the resulting vegetation unit is known as a *vegetation province* (Gleason, 1910: 42). The area of the province is generally uniform in physical conditions. This uniformity is only relative, being subject to gradual geographic variation in climate, perhaps giving rise to subregions in distant parts of the province, and to abrupt local variations in soil, water-content, exposure, etc., giving rise to local or edaphic plant assemblages very different from those of the climatic or geographic type. Thus the prairie province occupies the winter-dry interior region of North America. Environmental variations from east to west, climatic and physiographic, divide the province into the three subregions of Pound and Clements (1898). Certain plant species range over one or all of these subregions, still others establishing themselves over the whole area of the province and also scatteringly eastward, in dry treeless parts of the deciduous forest province, to the Atlantic coast. These last are also typical prairie plants, though

extra-limital in parts of an adjoining province locally approximating the prairie environment.

The habitat-selection of different animal species results, in precisely the same manner, in similarity of geographic range among ecologically similar animals. These correspondences of distribution point to the existence of definite areas characterized by general similarity of the animal assemblages. As the physical factors of the environment are the same ultimately for animals as for plants, and as the vegetational environment for animals has the same range as the physical environment, we might expect animal communities to have the same geographic distribution as plant communities, and we might expect the area of the plant province to be characterized by distinctive kinds of animals as well as by distinctive kinds of plants. The province is thus not simply a vegetation province, but a *biotic province*. This is not a new notion. Ruthven (1908: 388-390) has stated a current viewpoint as follows:

Those who are acquainted with the literature of the field zoology of North America are familiar with the fact that, since the time of the Pacific Railroad surveys, naturalists have noted that there are in North America well-defined biological regions. These have been pointed out at various times by Allen, Cope, Merriam, and others, and the fauna of each has been more or less investigated. . . . For example, we have forms of birds, reptiles and mammals characteristic of the southeastern deciduous forest region, and still others characteristic of the northeastern coniferous forest region, etc.

Shelford (A: 604) bases his classification of animal regions upon that of plant regions, as worked out by Schimper (1903) and Transeau (1903, 1905).

How close the correspondence of distribution of particular animals with that of vegetation provinces may be, is well shown in the case of North American rabbits (Nelson, 1909). The distribution maps shown for certain species and groups of these animals might almost serve as maps of the provinces. Many other animals, vertebrate and invertebrate, correspond in area with the plant provinces. Among the insects listed by Hart (1907: 205)

as western species, those for which a number of locality records are available are plainly to be assigned to the prairie province, the range of most of them extending west to the Rocky Mountains, north about as far as Montana, east to Illinois or Indiana, and south to Texas.

Other animal species bear apparently no relation to province boundaries. Such animals have been discussed by Shelford (*A*: 606, footnote), who shows them to be of three types: (1) Species of scattered but very wide range, covering perhaps several plant realms (animals of local associations of extreme habitats); (2) Species occupying only a part of the plant realm in which they belong (animals of such ecological constitution that their range is restricted by some conditions unfavorable in certain parts of the province); (3) Species occupying intermediate ground between two realms—these are few (Ruthven). These exceptional species are found also in plants, so that local associations are occupied by both plants and animals of the scattered-but-wide type of range, while certain subregions, as the Great Plains area of the prairie province, contain associations with both plant and animal species restricted to these less extensive areas.

Associations of two adjoining provinces may intergrade, if ecologically similar, or may alternate if dissimilar. Similar associations of two provinces may contain the same or closely related species, as with certain grasshoppers which range in both northeastern and western coniferous provinces (*D*: 173). But these same associations contain also plant species in common, so that irregularities of range are no greater in animals than in plants.

2. *Distribution Within the Province: Distribution of Plants and Animals into Communities.*—It is seen that plant and animal species may correspond closely in geographic range. There may be also more local correspondence in distribution. The plant community has been found by the writer to be the convenient index of the

area of the habitat for animals. It has been observed, in an area in Michigan, that grasshopper species correspond closely in local distribution with plant communities (*D*). There is evidence that local distribution of animals is seldom promiscuous as a result of motility (*D*: 159). It appears also that the local variability of environmental conditions within the area of the climatic plant community is sufficiently great, usually, to supply all necessary conditions for a large number of animals, so that the limits of the plant community need not be passed, ordinarily.

The animal community of the area may be thus, in large measure, self-contained, and coextensive with the plant community (*D*: 161).

One of the problems of plant ecology has been the differentiation of plant communities or associations. Mere comparison of lists of species is not sufficient; relative abundance of various species must be considered as well. Animal assemblages in contiguous areas must be separated in the same way. Given two adjoining habitats differing in plant population, it has been found that, in addition to differences of animal species,⁶ there are also differences of relative abundance in those animal species common to the two areas (*D*: 154, 167).

The local area of a plant community is determined by (1) local distribution of the physical environmental complex, and (2) influence (competition, etc.) of adjoining plant communities. Local area of the animal community depends upon (1) local distribution of physical environment, and (2) local distribution of vegetational environment, the latter being uniform over the area of the plant community. Contiguous areas differing in physical and vegetational conditions will be expected to differ also in animal population, in a degree comparable to that of the differences in environmental conditions.

Physical habitats, and plant communities, sometimes alternate, sometimes intergrade; it is not unreasonable to expect accompanying alternation or intergradation of

⁶ Differences in *species*, both plant and animal, are accompanied by differences in ecological constitution.

animal populations. Certain of the animal assemblages of sand habitats, as studied in central Illinois, intergrade; others, as oak forest and bunch-grass, differ radically.

The above considerations, if correct, appear to signify that, in ordinary climatic development of plant and animal life in temperate land environments, the area of the animal assemblage is that of the plant assemblage, both resting basically upon the physical environment. The plant and animal assemblages are therefore coextensive parts of a biotic association, composed of both plants and animals, and this association as a whole constitutes the real terrestrial community of living organisms.

B. LOCAL RELATIONS OF PLANT AND ANIMAL ASSEMBLAGES
(RELATIONS WITHIN THE ASSOCIATION)

The more intimate relations between plants and animals are seen in the detailed study of a single association. The bunch-grass association of sand prairie is selected for illustration (*E*: 68).

1. *Similarity of Ecological Type of Plants and Animals*.—Shelford has shown (*A*: 593-594) that animals and plants may evince ecological similarity by similar response to the same general environmental conditions, behavior responses in animals⁷ corresponding to structural responses in plants,⁸ so that *mores* of the animal may be in accord with *growth-form* in the plant. Shelford states (*B*: 87) that "plants and animal communities are in full agreement when the growth-form of each stratum of the plant-community is correlated with the conditions selected by the animals of that stratum."

In the bunch-grass there is general agreement, according to this criterion. The herbaceous stratum is occupied mainly by tuft and mat plants—bunch-grasses, cactus and a few half-shrubs. Associated with the tuft or mat growth-form is the sedentary mores of the plant-inhabiting animals (leaf-beetles, stem-borers, ambush-bugs, etc.). A considerable proportion of ground surface

⁷ Or motile organisms, cf. *C*: 305.

⁸ Or sessile organisms.

is bare sand; in the interspaces between the dominant plants are slender annuals (interstitial plants), and here are also found animals of the roving mores of the ground stratum (interstitial animals). Many of these are swift-running and predaceous (six-lined lizard, tiger beetles, lycosid spiders).

Correspondence in ecological type of plants and animals in the bunch-grass is not complete in several respects. Shelford mentions types of disagreement (*B*: 88; *C*: 306-308), and there is a further important kind of disharmony, in mixed associations, due to presence of diverse types of plants and animals (*D*: 163). Mixed associations are quite frequent in forest border regions, and in the transition area between two provinces. The plant and animal assemblages of a given habitat, particularly if climatic and extensive, are usually in general ecological agreement, and the exceptions are likely to be infrequent or temporary (Shelford, *B*: 88).

2. *Relative Dependence of Plant and Animal Assemblages.*—There is evidence that the agreement of plant and animal assemblages of terrestrial associations is often a matter of accommodation on the part of the animal assemblage. In the early stages of development of vegetation, local physical conditions dominate; in later stages the vegetation assumes the type determined by climatic conditions, and exerts nearly complete control over local physical factors. In established associations, therefore, the locally dominating environmental feature is the vegetation. Shelford states that in the several associations of a successional series, the dominating animal mores are correlated with the dominating conditions (*B*: 94) and that, as the forest increases in density, the animals make use of the vegetation in increasing degree, particularly for breeding-places, and as places of abode (*B*: 90). Many grasshoppers of open grassland depend upon a particular kind of soil for egg-laying, while those of closed forest lay eggs in fallen logs—a condition of the plant environment (*D*: 163).

The sand-prairie vegetation is in an intermediate stage, certain animals depending chiefly on the presence of loose bare sand, others on the bunch-grass vegetation. With development of bunch-grass into closed grassland, the interstitial animals are eliminated. The animals of established associations, while in accord with climatic physical conditions, are perhaps more intimately affected by vegetation conditions. Since established associations are very much more extensive than primitive associations, the importance of vegetation as a dominating part of the environment for animals becomes apparent, and we may conclude that the character of the plant assemblage determines, to a large extent, the ecological type of the animal assemblage.

3. *Correspondence in Distribution within the Association.*—The uniformity of physical and vegetational conditions is only relative. There are spots in the bunch-grass association in which local invasion of blue grass has occurred, darkening and binding the soil. In such partly humified situations, small colonies of the cornfield ant, not occurring elsewhere in the bunch-grass (*E*: 57), have been found. There are also areas some few feet in diameter in which the bunches of grass are few, small and scattered. In these relatively bare patches the abundance of interstitial animals is greatly increased. More direct relations are seen in the case of animals associated with particular species of plants. Within the association, any animal species, like any plant species, may be distributed generally throughout the area, or it may be restricted to a part of the area characterized by a slight environmental difference, or it may occur in scattered parts of the association, characterized by scattered local differences (*D*: 168). There is evidence that, in so far as the vegetational environment is concerned, distribution of animals within the association is usually a direct function of similar distribution of plants.

4. *Uniformity of Species Composition of Plant and Animal Assemblages.*—It has been seen that plant assem-

blages of definite ecological type, as regards growth-form, etc., are regularly accompanied by animal assemblages of similar ecological type, as regards mores. Interest attaches also to the problem whether associated plant and animal assemblages show definite *species* relations.

One familiar with a certain association, who visits a representation of that same growth in a different part of the same climatic region, will be struck with the fact that a large proportion of both plant and animal species is well known, while a certain proportion, perhaps considerably smaller, is new to him. The writer has been impressed with the similarity of the plant and animal populations of the sandhills of central Nebraska and of eastern Colorado, to those of the sand prairie of central and western Illinois, despite the fact that certain species are not common to the two areas. Tiger-beetles, blow-snake, grasshoppers, box-turtle, six lined lizard, western meadow-lark, white-footed mouse, among the animals; prickly-pear, lead-plant, bunch-grasses, sand-bur, sand evening primrose, among the plants; are represented in the two areas either by the same or by closely related varieties and species. There are no yuccas or sand-sages in the Illinois sand prairie, no lizard *Holbrookia* nor lubber-grasshopper *Brachystola*; and there are certain eastern species not found in the western sandhills. But on the whole the species (particularly the important species) common to the two areas are more numerous. This is the more remarkable in view of the fact that distribution of sand prairie is discontinuous, the largest, nearly uninterrupted gap being several hundred miles in extent. Many of the animals, as well as plant species, of dry mixed prairie-grass in loamy soil, are the same along the mountain-front in Colorado (Vestal, 1914b) as in north-central Illinois. The likenesses become much more impressive as distance is decreased.

Absolute identity of species composition, where large numbers of species are involved, is an ideal condition,

never actually attained. No one can say just what proportion of species-in-common is necessary for two growths to be said to represent the same association. In addition to likenesses and differences of environment, of aspect, and of history, which must be weighed, the different plant and animal species vary so much in importance in the association, in physiological variation and in range of environmental tolerance, that associations can hardly be separated or placed together on a statistical basis. A comparison of species is fair if the following kinds of plants and animals are left out of consideration; (1) those of limited range within the climatic region or province, including species belonging more properly to other provinces; (2) those of very indefinite habitat-relations, which are found in nearly any kind of habitat; (3) those of special restricted habitats, which may be scattered about in many kinds of associations, as moist dead wood, in which particular fungi, beetles, perhaps snails, myriopods and pill-bugs, are usually found; or as excrement of grazing animals, in which certain molds, certain dipterous and scarabæid larvæ, etc., regularly occur, irrespective of surrounding conditions; (4) invaders from nearby associations; (5) ruderal and introduced species; and possibly one or two other groups. The second and third groups may be called the irregular element; the fourth and fifth may be known as the derived element. While these groups make a formidable list, their representatives constitute usually a very small proportion of the organisms of the association. The other organisms, and some of these, follow habitat-differences, as represented in different associations, very closely.

Since hardly any two species are identical in habitat-relations, geographic and even local variation must be looked for, but since many species resemble each other more or less closely in general ecological relations, there come to be recognized certain ecological groups of species, each characterized by a general type of growth-form in plants, or by a general kind of mores in animals, and

these groups may be considered to be small or large, according as we emphasize minor differences or general likenesses.

Now within any limited region (let us postulate first an area removed from the influence of an adjoining province) there are only a limited number of ecological groups, of growth-forms of plants, and of mores among animals, each group represented by a limited collection of species. Each habitat within this restricted area will be characterized by definite physical conditions, and with these will be correlated certain growth-forms of plants and certain mores of animals, each represented by as many of the species as can migrate into and survive within the area, as determined first by capabilities of migration and by habitat-selection, and second by interrelation of species and of individuals. It follows that physical complexes which are alike will become populated with similar complexes of ecological groups, represented by similar collections of plant and animal species, and that unlike physical areas will be occupied by different combinations of ecological groups, and will be composed of different species. Two areas within this region which have similar physical conditions and similar plant growths will be expected to have a large number of animal species in common, although direct relations between species of animals and species of plants obtain only rarely (between comparatively few associated plant-and-animal pairs). It is to be noted that species composition of the animal assemblage varies proportionately no more widely than does that of the plant assemblage.

No terrestrial continental region is sufficiently isolated to be free from influence of surrounding areas, and since the influences are different from different directions, and since there is continual change of physical conditions, and of range and abundance of plant and animal species, there must be more or less local and geographic variation of species composition within similar but separated habitats. Geographic variation is wider with distance.

because the geographic and physiographic complexes vary geographically, as well as the entire collection of plant and animal species which may invade the habitat. Within the area of the climatic province, however, or at least within the area of a subregion of the province, climatic, physiographic and biotic complexes are likely to be relatively constant, that is, likenesses of two areas are likely to be greater and more striking than differences. Within the province or subregion, therefore, it is to be expected that species composition of association of closely similar habitats will be relatively constant. Particular plant and animal assemblages will be found together, both associated with a particular habitat. Field observation bears out these expectations.

Conditions within the transition zone between two climatic regions or provinces are much more complex than in an area in the middle of a sub-region or province; climatic and physiographic conditions vary to wider extremes and are less stable; the total number of species near enough at hand to invade a given habitat is much greater. Mixed associations, often transitional as regards physical conditions, are composed of representatives of both provinces. Animals of a particular association of one province, may be found with plants of a similar or equivalent association of the other province. When *three* geographic elements are represented, as at the southern end of Lake Michigan (cf. *C*, and Vestal, 1914*a*), the complication of conditions is extreme. Even here, on the dry sand of old lake beaches, fairly typical representations of sand prairie can be seen; and though such habitats are shared with deciduous forest associations, and with associations of the northeastern coniferous forest province, and with mixed associations, the bunch-grass growth can still be recognized in dry shifting sterile sand, with bunch grass plant species, and bunch-grass animal species. The tendency towards uniformity of association of plant and animal assemblages is even here to be made out.

If the foregoing considerations relating to relations between plant and animal communities are correct, the thesis mentioned at the beginning of part V would seem to be justified, though the evidence is far from complete. Plant and animal assemblages are mutually interdependent; the plant assemblage dominates in established associations. Plant and animal assemblages correspond in geographic distribution, in distribution into communities, and in more detailed distribution within the habitat. They are made up of ecologically similar groups correlated with the same physical conditions or with each other. Though there are few direct relations between particular species of plants and animals, it so happens that within any restricted region, particular collections of animal species come into regular association with particular collections of plant species, the species composition within the habitat exhibiting a greater or less degree of uniformity, except for minor irregular and derived elements. The more restricted, or uniform in biological conditions, this region is, the greater the uniformity of the collection of species. Climatic and extensive associations, and established associations, show a greater degree of uniformity than local or primitive associations.

VI. SUMMARY AND CONCLUSIONS

The discussion is based principally upon the writer's study of prairie associations, the bunch-grass association of sand prairie in Illinois being chiefly used for illustration. Internal activities of the association are a complex of activities of all the organisms. Environmental influences are of three classes, physical, plant and animal. The characters of plants and animals are interpreted in their relation to these influences. Characters of plants may be classed as structural, physiological, biographical and numerical. Animals have, in addition, behavior or psychological characters. These groups of characters are intimately related, one to another. The relations of the animal to its animal-environment are of two kinds,

social and antagonistic, the latter relations being with food-species, competitors and enemies. Correlations of the various kinds of characters with relations involving food, competition and enemies, are given. According to its ecological constitution, each organism finds a status in the association, the whole being a self-contained and self-regulating system of activities.

Dependencies within the association are concerned mainly with sources and interchange of material and energy. Dominant plants (the most influential species) are those most intimately correlated with physical environment, as indicated by aggressiveness, abundance, frequency, size, etc. Dominant animals are most numerous among phytophagous forms. Dominance in an animal species includes dependence of other animals upon it (for food) plus the ability to thrive in spite of the drain upon its numbers. The degree of specialization of behavior is a convenient index of the relative influence of animals in the association. The dominant animals are moderately specialized, and carry on the ordinary work of the association. The highly specialized animals make use of space otherwise unoccupied, and food material not available to other species, or not taken by other forms. Least highly specialized animals act as a check upon undue departure from biotic equilibrium.

The association may be divided into minor groups of organisms, both in space and in time. Space-division is vertical, resulting in strata, and horizontal, resulting in sub-habitats of greater or less magnitude. The strata and sub-habitats present a larger or smaller degree of discontinuity and of internal variability. Time-distribution is diurnal, seasonal and annual. There are also time-variations produced by variability of weather conditions and by oscillatory disturbances.

The relations between plant and animal assemblages have long been known, in a general way, to be intimate. Plants and animals agree in similar response to common environmental influence, and in types of geographic dis-

tribution. Upon investigation, it begins to appear that plant and animal assemblages are coextensive parts of a biotic association, composed of both plants and animals, and this association as a whole constitutes the real terrestrial community of living organisms. Plant and animal assemblages are mutually interdependent; the plant assemblage dominates in established associations. Plant and animal assemblages correspond in geographic distribution, in distribution into communities, and in more detailed distribution within the habitat. They are made up of ecologically similar groups correlated with the same physical conditions or with each other. Though there are few direct relations between particular species of plants and animals, it so happens that within any restricted region, particular collections of animal species come into regular association with particular collections of plant species, the species composition within the habitat exhibiting a greater or less degree of uniformity, except for minor irregular or derived elements. The more restricted in area, or uniform in biological conditions, this region is, the greater uniformity of the collection of species. Climatic and extensive associations show a higher degree of uniformity than local or primitive associations.

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SHORTER ARTICLES AND DISCUSSION

ANOTHER HYPOTHESIS TO ACCOUNT FOR DR. SWINGLE'S EXPERIMENTS WITH CITRUS

THE results of the cross-breeding experiments with forms of *Citrus* by Walter Swingle have given rise to quite a number of different hypotheses, to account for the facts observed.

The facts are simply these. All the different forms of *Citrus* used in the experiments, *Citrus trifoliata*, the lemon, orange and other citrous fruits have, so far, proved to reproduce their own type through seed.

Nevertheless, the plants raised from one single cross are exceedingly different among themselves. And yet, all these new forms, for so far as tested, have proved truly to reproduce their own kind only, if sown.

The theories offered to account for these facts are rather complex. So far, we have not seen the simple hypothesis which we want to add to the others.

The fact, that the F_1 from almost every cross between types of *Citrus* is multiform, can only be accounted for on the assumption, that the parent plants are impure (heterozygous) for a number of genes. The difficult question is this: how can a tree, impure for a number of genes, produce seed which always only reproduces the type? We know, that if a plant reproduces itself by an asexual method, all its daughter plants are pure for those genes in respect to which it was pure, impure for those genes for which it was impure. Is it possible that in these trees the seeds normally produced are not derived from a union between two normal gametes? In *Citrus*, with its adventitious embryos, this is very well possible. If the forms of *Citrus* used by Dr. Swingle are self-sterile, the seeds normally produced by these trees, are not produced by the union of two gametes, but as buds, asexually.

This hypothesis, that the *Citrus* used are self-sterile, and that the seeds normally produced, are produced asexually, fully accounts for all the facts. All the daughter plants from uncrossed seeds are genotypically identical with the mother plant, as in all clones. On pollenization by another tree, normal seeds are produced, each the result of the union of two real gametes.

These seeds contain different combinations of the genes, for which the parent plants are impure, as normally. The F_1 generation for this reason becomes as diverse as such generations always are, if the parents are impure for numerous genes.

But these daughter plants, although impure for a number of genes, can, because of their self-sterility, in their turn only produce seed asexually and therefore their offspring will be like themselves.

It should not be difficult to test our hypothesis. It seems easier to find out, whether the seeds produced without crossing in *Citrus* contain the embryo formed by fertilization of the embryo sac, or embryos formed adventitiously by the adjacent tissue, than to test any of the other theories, which assume a peculiar behavior of the chromosomes.

Our hypothesis, that a variable F_1 , of only true-breeding plants (from the union of two true-breeding forms), results from habitual self-sterility and asexual production of seed, with real fertilization in the case of a cross taking place, not only accounts for the facts found by Swingle, but also for those found by Rosen with *Erophila verna*. These facts were somewhat different. The F_1 plants were all identical, and somewhat intermediate. They gave rise to a variable F_2 generation of which all the plants bred true to their type. These facts can be explained on the assumption, that *Erophila verna* is self-sterile, and that, in the absence of cross-fertilization, unfertilized egg-cells develop parthenogenetically. Such F_1 plants, which are impure for a number of genes, should therefore produce as many different kinds of F_2 plants, as there are female gametes produced, and in the same proportions. In the case of such a plant being impure for two genes, we should expect it to produce plants of the four different types, not in the usual proportion of 9:3:3:1, but in equal proportions, 1:1:1:1. The F_2 plants from such seed could only be pure for all the genes present.

It would be possible in *Erophila verna* to find out whether F_1 plants, impure for two genes, produced daughter plants of the four kinds, AB , Ab , aB , and ab , in the proportion of 9:3:3:1, or in proportion 1:1:1:1, and thus to test our hypothesis.

To find out, whether it is possible, that a plant, impure for a number of genes, produces a variable F_2 generation of only completely homozygous plants, we have begun a series of experiments with squashes. Some hybrid plants have not produced a

single fruit from carefully sealed female buds, others have given plenty of empty fruit, but some hybrids have produced several fruits, full of viable seed. If this seed is formed by the parthenogenetic development of unfertilized normal egg-cells, as we have reason to believe, we expect to raise a variable F_2 generation of exclusively homozygous plants. If these seeds have developed by apogamy, or any other asexual process, we expect to obtain a second generation consisting exclusively of plants like the original hybrids. Thus we will have a non-cytological test to decide between apogamy and true parthenogenesis.

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BUSSUM, HOLLAND,
March 18, 1914

